

BIOSYSTEMATIC STUDY AND TYPIIFICATION OF THE CALIFORNIAN COREOPSIS (COMPOSITAE) SECTIONS *TUCKERMANNIA*, *PUGIOPAPPUS*, AND *EULEPTOSYNE*

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ABSTRACT

Biosystematic study and study of type and other material of the eight species of Californian *Coreopsis* (sections *Tuckermannia*, *Pugiopappus*, and *Euleptosyne*) was undertaken. The group is resistant to the biosystematic approach, in the sense that artificial hybridizations attempted in all combinations among the species were mostly unsuccessful. Only *C. maritima* X *C. gigantea* hybrids (and the reciprocal) were produced and these had high pollen stainability. All eight species in the three sections are $n = 12$. The perennials (section *Tuckermannia*) have noticeably larger meiotic chromosomes than do the annuals (sections *Pugiopappus* and *Euleptosyne*). The three sections are well-differentiated and deserve sectional status. A key to the taxa and citation of observed types and other specimens examined is presented. Based on selected morphological characteristics, the relative evolutionary advancement of the species within each section is postulated.

INTRODUCTION

This paper continues a biosystematic study of *Coreopsis* (Compositae) and will largely complete work on the biosystematic aspects of the North American species of *Coreopsis* north of Mexico. Earlier papers have included, for examples, work on *C. saxicola* (Smith, 1973), the disk flower lobing and sectional status of North American *Coreopsis* (Smith, 1972), a description of a new species (Smith, 1974), and a biosystematic survey of the eastern United States and Canadian species of the genus (Smith, 1976). Some recent work has involved collaborative chemosystematic study, for examples, flavonoid chemistry of section *Palmatae* of *Coreopsis* (Crawford, Smith, & Mueller, 1980), of selected species in section *Coreopsis* (Crawford & Smith, 1980; Smith & Crawford, 1981) and at the sectional level in North American *Coreopsis* (Crawford & Smith, 1983a), allozyme variation in certain species pairs (Crawford & Smith, 1982a, b) and in the varieties of *C. grandiflora* (Crawford & Smith, 1984a), and anthochlor floral pigments in North American *Coreopsis* (Crawford & Smith, 1983b). Phyletic trends of the sections of North American *Coreopsis* were suggested earlier (Smith, 1975).

This paper is concerned with the results of biosystematic study and typi-

fication of the Californian *Coreopsis*, a group of eight species in three sections limited largely to California. Two of the species range into Arizona and Baja, California, Mexico. A new variety of *C. californica*, endemic to Arizona, was recently described by the author (Smith, 1983). This group was the subject of an excellent paper by Sharsmith (1938) that clarified the morphology and ranges of the species but which did not clearly typify the species in the group. The group was also treated as part of the genus (Sherff, 1936) and part of the North American portion of the genus (Sherff, 1955), also without clear typification. Recent leaf flavonoid studies of sections *Pugiopappus* and *Euleptosyne* (Crawford & Smith, 1984b) provide chemical data that are not concordant with the clearcut morphological differences between these two sections. The present paper will not be concerned with detailed morphological descriptions or illustrations of the species, since these were generally well-presented by Sharsmith (1938), but with the results of biosystematic study of the species, with the probable relative evolutionary advancement of the species within each section, and with the typification of the species in the group.

MATERIALS AND METHODS

Live material, achenes, and preserved buds of the species were collected in 1980 and 1981 on field trips to Arizona, California, and Baja California. Live material was transplanted to the greenhouse, or raised from field-collected achenes (one sample each of *C. gigantea* and *C. maritima* was kindly furnished by the Rancho Santa Ana Botanic Garden). Artificial hybridizations were attempted in all combinations in the greenhouse. Heads were bagged with lens paper prior to anthesis. They were uncovered briefly after anthesis of the outer few rows of disk flowers, and the pollen-covered disk-flower stigmas of the respective parents were gently rubbed together and then rebagged until fruit set. Some heads of each species were bagged and left bagged to check for self-compatibility. Selected crosses were attempted between the Californian species of *Coreopsis* and species of other sections, to check for intersectional crossability.

Germination of achenes, especially of the annual species, was poor under standard procedures (on moist filter paper in petri dishes), but reasonably adequate germination was obtained by leaching the achenes in a cheesecloth bag for three days in running tap water, then dissecting out each embryo (onto moist filter paper in petri dish). All seedlings were transplanted into a half soil/half sand mixture in clay pots in the greenhouse.

Buds harvested in the field and greenhouse were squashed by the anther squash technique in 1% propiocarmine stain after fixation for one to several days in a modified Carnoy's fixative (ethyl alcohol, propionic acid, chloroform; 3:1:1), as in previous papers in this series (e.g. Smith, 1983, 1982).

Percentage pollen stainability of the parental and hybrid stock was tested in analine blue (alcohol soluble, 1% by weight in 90% propionic acid/

water), with a minimum of 300 pollen grains scored per individual; deeply blue grains were counted as stainable and pollen stainability was equated with fertility.

Herbarium material of the eight species was examined from nine herbaria in California and Arizona and from PH. In addition, some of these herbaria and 16 other herbaria were contacted in attempts to locate and examine type material of all of the California species of *Coreopsis*.

RESULTS AND DISCUSSION

Biosystematic work:

All eight species grew and flowered in the greenhouse soil mixture, indicating that the odd habitats where some of them are often found (e.g., serpentine soils for *C. douglasii*, shale slopes for *C. hamiltonii* and *C. bigelovii*) are not obligate for the species. One species, *C. gigantea*, tended to die from root rot unless planted directly in the ground in the greenhouse.

All species of the three sections have high pollen stainability (90–99%), and all are self-incompatible as judged by failure of fruit set in bagged heads that were left bagged. *Coreopsis gigantea* and *C. bigelovii* exhibited a low level of selfing when stimulated by pollen from another species.

Approximately 20 intersectional hybridizations were attempted between various Californian species of *Coreopsis* and species in other sections (sect. *Coreopsis*, *Calliopsis*, *Eublepharis*, *Palmatae*, *Electra*, *Anathysana*, and *Pseudoagarista*). All intersectional hybridizations failed.

All eight species of the three sections are $n = 12$ (Fig. 1). The meiotic chromosomes of the perennials (sect. *Tuckermannia*) are much larger and easily distinguishable from those of the annuals (sect. *Pugiopappus* and *Euleptosyne*), but the chromosomes of each subgroup (annuals or perennials) are not easily distinguishable among themselves.

The California *Coreopsis* group is resistant to biosystematic analysis, in the sense that only one of the 28 possible artificial hybrid combinations (lumping reciprocals) was successful. The *C. maritima* X *C. gigantea* cross was reciprocally successful and produced several artificial F_1 hybrids. Only seven of these have flowered. They have the large, thick-stemmed, sprawling habit of *C. gigantea* but form few and large heads on elongate peduncles as in *C. maritima*. The average pollen stainability of the seven F_1 hybrids was 95%, falling within the range of the normal pollen stainability of the parental species. Several F_2 and BC_1 hybrids (*C. maritima* the repeating parent) are under cultivation, but most of these have not bloomed yet. Four F_2 hybrids (resembling *C. gigantea* or the F_1) averaged 65% pollen stainability, and five BC_1 hybrids (resembling *C. maritima*) averaged 92% pollen stainability. Such high fertility in both first and second generation hybrids between *C. maritima* and *C. gigantea* strongly suggests that *C. gigantea* should be reduced to a variety of *C. maritima* (the older name). However, since

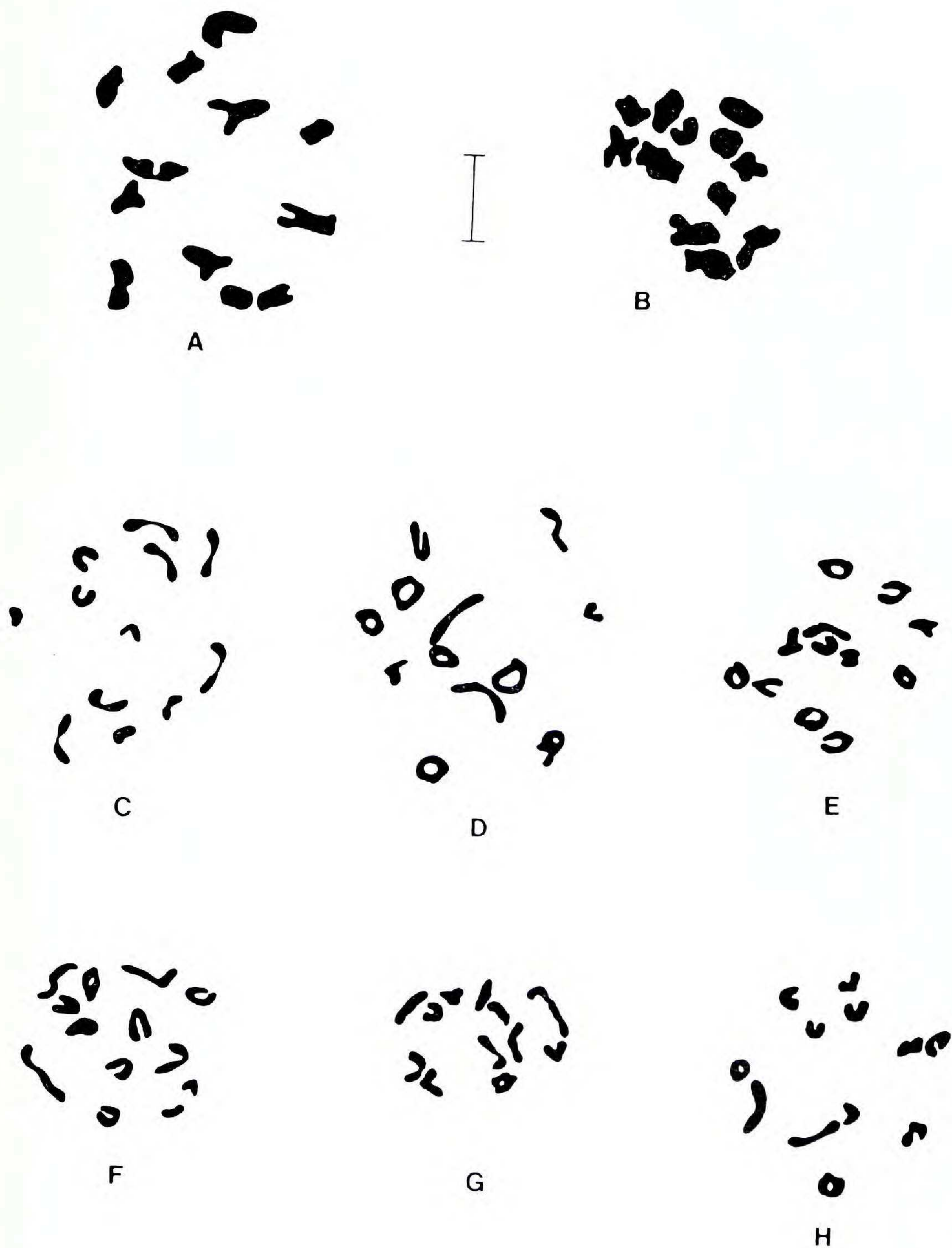


Figure 1. Meiotic configurations (diakinesis) of the Californian *Coreopsis*; inked-in tracings from photographs. Top row = section *Tuckermannia*, middle row = section *Pugiopappus*, bottom row = section *Euleptosyne*; A = *C. gigantea*, B = *C. martima*, C = *C. calliopsidea*, D = *C. bigelovii*, E = *C. hamiltonii*, F = *C. stillmanii*, G = *C. dogulasii*, H = *C. californica* var. *californica*; all $n = 12$; reference bar = 10 μm .

I noted no natural hybrids in the field or in herbarium materials, and the ranges of the two do not overlap (cf. Sharsmith, 1938), it seems best to maintain *C. gigantea* at the species level.

Key and taxonomic treatment:

Below is a key (modified from Sharsmith, 1938; in part from Smith, 1983) to the taxa of sections *Tuckermannia*, *Pugiopappus*, and *Euleptosyne*, followed by a taxonomic treatment including typification, brief descriptions, comments on relative evolutionary advancement of the species within each section, and citation of specimens examined. Blooming times are not indicated, since all eight species bloom mostly in the period March-May.

1. Plants perennial, commonly 3–20 dm tall; heads (measured from ligule tip to the opposite ligule tip) medium-sized to large, commonly 4–10 cm wide; ligules 10–20, elliptical-oblong to elliptical-oblongate; coast and offshore islands (section *Tuckermannia*).
2. Heads several to many and medium-sized (ca 4–8 cm wide), cymosely clustered, on peduncles ca 6–20 cm long; stem solid; Los Angeles County to Monterey County and adjacent islands (and Guadalupe Island, Mexico) 1. *C. gigantea*
2. Heads few (ca 2–4) and large (ca 6–10 cm wide), on peduncles ca 15–50 cm long; stem hollow; San Diego County to Baja California Norte and nearby adjacent islands 2. *C. maritima*
1. Plants annual, commonly 0.8–4.0 dm tall; heads (measured as above) small to medium-sized, ca 1–7 cm wide; ligules 5–12, obovate; mountains and deserts.
3. Achenes dimorphic, the ray achenes glabrous and epappose, the disk achenes antrorsely villous, ciliate, and aristate with two aristae (section *Pugiopappus*).
4. Outer phyllaries ovate; pappus aristae ca 4 mm long 3. *C. calliopsidea*
4. Outer phyllaries linear-oblong; pappus aristae ca 0.9–2.8 mm long.
5. Pappus aristae ca 1.7–2.8 mm long; chaff basally adnate to and falling with the disk achenes; ligules remaining horizontal in full anthesis 4. *C. bigelovii*
5. Pappus aristae ca 0.9–1.3 mm long; chaff free from and falling separately from the disk achenes; ligules at first horizontal, becoming reflexed in full anthesis 5. *C. hamiltonii*
3. Achenes monomorphic, both ray and disk achenes epappose, eciliate, and more or less bearing tiny short-clavellate trichomes (section *Euleptosyne*).
6. Leaves flat, pinnate to bipinnate into spatulate lobes ca 1–3 mm wide; outer phyllaries bearing few to several tiny, setose, gland-tipped teeth on the margins near the base 6. *C. stillmanii*
6. Leaves linear-filiform, entire or with a few linear-filiform lobes, the leaves (or lobes) 0.3–1.3 mm wide; outer phyllaries lacking gland-tipped teeth basally.
7. Achenes shining, glabrous or nearly so, the body dark brown and lacking reddish-brown (blackish) spots, the wing thin 7. *C. douglasii*
7. Achenes dull, bearing several to many tiny short-clavellate trichomes, the body tan to brownish or reddish and commonly

with several to many reddish-brown (blackish) spots (best seen on immature achenes), the wing at least partially corky-thickened.

8. Mature achenes 3.0–4.3 mm long, the wings 0.3–0.7 mm wide and corky-thickened throughout; immature achenes with 0–few reddish-brown (blackish) spots in a single row at each margin of the body; southern California and Baja California, Mexico 8a. *C. californica* var. *californica*
8. Mature achenes 4.6–6.3 mm long, the wings 0.8–1.5 mm wide and corky-thickened near body but thin near margin; immature achenes with numerous reddish-brown (blackish) spots more or less scattered on the body (not confined to a single row at each margin); Arizona .. 8b. *C. californica* var. *newberryi*

Section TUCKERMANNIA (Nutt.) Blake, Proc. Amer. Acad. 49:340. 1913.

Tuckermannia Nutt., Trans. Amer. Phil. Soc. II. 7:363, as genus. 1841.

Leptosyne sect. *Tuckermannia* A. Gray, Bot. Calif. 1:356. 1876.

TYPE SPECIES: *Coreopsis maritima* (Nutt.) Hook f.

1. COREOPSIS GIGANTEA (Kellogg) H. M. Hall, Univ. Calif. Publ. Bot. 3:142. 1907.

TYPE: U.S.A. CALIFORNIA. Santa Barbara Co.: Santa Rosa Island, bottom of Cherry Canyon, 5–7 Apr 1960, P. H. Raven 14965A (NEOTYPE, here designated: JEPS!).

Leptosyne gigantea Kellogg, Proc. Calif. Acad. Sci. 4:198. 1873. TYPE: U.S.A.

CALIFORNIA: Cuyler Harbor on San Miguel Island, W. G. W. Harford s.n., not located.

Tuckermannia gigantea (Kellogg) M. E. Jones, Contr. W. Bot. 15:74. 1929.

Additional specimens examined: U.S.A. CALIFORNIA. Los Angeles Co.: 29 Apr 1918, *Evermann* s.n. (CAS); *Fosberg* S4420 (PH, two sheets); *Grant* 680-2228 (PH); *Raven* 13852 (JEPS), 17848 (UC); Jan & Feb 1903, *Saunders* s.n. (PH); *Thomas* 484 (DS), 6503 (DS); *Wolf* 3631 (LA). Monterey Co.: *Balls* 12191 (UC); 24 May 1923, *Walther* s.n. (CAS). San Luis Obispo Co.: *Chisaki & Kamb* 1811 (UC). Santa Barbara Co.: *Abrams & Wiggins* 129 (CAS); *Breedlove* 2821 (DS); *Ferris* 7572 (UC); *Fosberg* S953 (PH), S1982 (PH), S2334 (PH), 7568 (LA, PH); Jul & Aug 1886, *Greene* s.n. (PH); *Keck & Hiesy* 5112 (DS); 24 May 1918, *Miller* s.n. (CAS); *Wiggins* 3487 (DS). Ventura Co.: *Bacigalupi* 5776 (JEPS); *Bright* 8134 (UARK); *French* 320 (UC); *Howell* 3793 (CAS); 20 Jun 1970, *Pollard* s.n. (CAS); *Shreve* 8207 (ARIZ); *Smith* 3584 (UARK), 3604 (UARK, two sheets); *Thompson* 1861 (JEPS); *Wheeler* 488 (DS). MEXICO. Baja California: *Kuijt et al.* 1049 (UC); *Moran* 2923 (DS); *Palmer* 41 (PH).

A large (commonly 1–2 m tall), fleshy-stemmed (the stem commonly 4–10 cm in diameter) and many-flowered (heads 4–8 cm wide) perennial with finely dissected leaves (ultimate segments ca 0.5–1.5 mm wide), of rocky cliffs and seacoasts of southern California on the mainland and offshore islands, from Los Angeles County and Santa Catalina Island north to Santa Rosa Island and Monterey County (also known from Guadalupe Island, Mexico).

Because of its larger growth habit and numerous heads, I consider this species to be the more primitive one in section *Tuckermannia*.

2. *COREOPSIS MARITIMA* (Nutt.) Hook. f., Bot. Mag. t. 6241. 1876.

TYPE: U.S.A. CALIFORNIA. San Diego Co.: On shelving rocks, near the sea at St. Siego, in upper California, *Nuttall s.n.* (LECTOTYPE, here designated: BM!).

Tuckermannia maritima Nutt., Trans. Amer. Phil. Soc. n. ser. 7:363. 1841.

Leptosyne maritima (Nutt.) A. Gray, Proc. Amer. Acad. 7:358. 1868.

Additional specimens examined: U.S.A. CALIFORNIA. San Diego Co.: *Bacigalupi* 5786 (JEPS); *Bartram* 586 (PH); *Clements & Clements* 226 (PH); *Dunn* 824 (LA); 30 Mar 1932, *Epling & Robison s.n.* (LA); *Lewis* 1220 (LA); *Moran* 2091 (UC), 2095 (UC); 25 Apr 1882, *Pringle s.n.* (PH); *Smith* 3585 (UARK); *Thomas* 6975 (DS); *Wolf* 1929 (ARIZ, CAS, DS, UC). MEXICO. Baja California: *Chandler* 5123 (UC); *Cooper* 2144 (UC); 1 Apr 1947, *Copeland s.n.* (DS); 5 Mar 1971, *Cummins s.n.* (ARIZ); 27 Mar 1940, *Epling & Robison s.n.* (LA); 7 Apr 1936, *Epling & Stewart s.n.* (DS, LA); 7 Apr 1951, *Flemming s.n.* (UC); *Fosberg* 51123 (PH); *Hendrickson* 4591 (ASU), 4612 (ASU); *Jones* 3134 (DS, PH, UC), 10 Jun 1926, *Jones s.n.* (DS); *Kappler* 798 (LA); *Moran* 3059 (UC), 8282 (DS, UC), 10556 (DS); *Smith* 3586 (UARK), 3587 (UARK); *Thomas* 12 (DS); *Wiggins* 5112 (CAS, DS, UC), 11971 (UC), 11985 (DS, UC), 13062 (DS).

A smaller (mostly 0.3–0.8 m tall), hollow-stemmed (the stem commonly 1–2 cm in diameter), and few-flowered (heads 6–10 cm wide) perennial from a carrot-like root with less finely dissected leaves (ultimate segments ca 1–4 mm wide) of rocky seacoasts of Baja California and offshore islands and of San Diego County, California.

Because of its smaller size, semi-scapose habit, and fewer heads, I consider this species to be the more advanced member of section *Tuckermannia*. *Coreopsis maritima* has the largest heads of all North American species of the genus. The scapose habit in North American *Coreopsis* is considered a derived condition and is often accompanied by increase in head size.

Section *PUGIOPAPPUS* (A. Gray) Blake, Proc. Amer. Acad. 49:340. 1913.

Agarista DC., Prodr. 5:569, as genus. 1836 (but not of other authors).

Pugiopappus A. Gray in Torr. Pacif. Railr. Rep. 4:104, as genus. 1857.

Leptosyne sect. *Pugiopappus* A. Gray, Syn. Fl. N. Amer. 1(2):300. 1884.

TYPE SPECIES: *Coreopsis calliopsidea* (DC.) A. Gray

3. *COREOPSIS CALLIOPSIDEA* (DC.) A. Gray, Bot. Mex. Bound. 90. 1859.

TYPE: U.S.A. CALIFORNIA: without locality, *Douglas* 49 (LECTOTYPE, here designated: BM!; ISOLECTOTYPES, here designated: K two sheets!).

Agarista calliopsidea DC., Prodr. 5:569. 1836.

Pugiopappus calliopsidea (DC.) A. Gray, Proc. Amer. Acad. 8:660. 1873.

Leptosyne calliopsidea (DC.) A. Gray, Syn. Fl. N. Amer. 1(2):300. 1884.

Leptosyne calliopsidea var. *nana* A. Gray, Syn. Fl. N. Amer. 1(2):300. 1884.

TYPE: U.S.A. CALIFORNIA. San Bernardino Co.: At Mohave station, etc., *Pringle s.n.* (LECTOTYPE, here designated: CAS!; ISOLECTOTYPES, here designated: F two sheets!, GH!, MO!, NY!).

Additional specimens examined: U.S.A. CALIFORNIA. Alameda Co.: *Carter* 777 (DS); *Eastwood & Howell* 1939 (DS); *Hoover* 1750 (JEPS). Fresno Co.: *Hoover* 4779 (JEPS, UC). Kern Co.: *Abrams* 11184 (DS); *Alva* 1868 (JEPS); *Davy* 1871 (UC); *Ferris* 9036 (DS, UC), 9131 (DS); *Fosberg* S1134 (PH); *Gould* 901 (ARIZ); *Heller* 7723 (DS two sheets, PH, UC); *Keck & Clausen* 3177 (DS); *Meng* 516 in part (CAS); *Smith* 3493 (UARK two sheets), 3579 (UARK); *Twisselman* 15062 (CAS two sheets), 15129 (CAS); *Wiggins* 9559 (DS); *Wolf* 6360 (ARIZ, LA). Kings Co.: *Bacigalupi & Macbride* 3547 (CAS, DS, JEPS); *Hoover* 4269 (JEPS, UC). Los Angeles Co.: *Bacigalupi* 4816 (JEPS); *Holmgren & Holmgren* 7625 (ASU); *Wolf* 8522 (ARIZ, DS, LA). Merced Co.: *Lyon* 1039 (UC). Monterey Co.: *Hoover* 2983 (DS, JEPS, UC). San Benito Co.: 24 Apr 1940, *Carpenter s.n.* (JEPS). San Bernardino Co.: 8 Apr 1938, *Beal s.n.* (JEPS); 6 Apr 1936, *Lewis s.n.* (LA); *McLeod et al.* 12141 (ASU); *Nordstrom* 348 (UC); *Smith* 3577 (UARK); *Tilforth et al.* 1556 (UC); *Twisselmann* 12050 (CAS two sheets, JEPS). San Joaquin Co.: *Hoover* 2869 (JEPS, UC). San Luis Obispo Co.: *Breedlove* 1979 (DS); *Fosberg* S1226 (PH); *Hoover* 10279 (UC), 11037 (UC); *Jepson* 16223 (JEPS); *Keck & Clausen* 3090 (DS two sheets); *Raven* 16965 (DS); *Twisselmann* 556 in part (CAS), 1758 (CAS). Santa Barbara Co.: *Breedlove* 1940 (DS); *Keck* 2243 (DS two sheets); *Muntz* 13619 (DS); *Raven* 16985 (DS two sheets, JEPS). Stanislaus Co.: *Hoover* 857 (JEPS); *Sharsmith* 1593 (UC). County not specified: *Anderson* 107/64 (UARK); 14 May 1882, *Pringle s.n.* (K, PH two sheets).

An annual commonly 10–40 cm tall, with leaves borne up the stem, ovate outer phyllaries (ca 4–5 mm wide), large heads (mostly 3–7 cm in diameter), chaff attached to the disk achenes, and aristae of the disk achenes ca 4 mm long, of sandy open soils of western San Bernardino and northern Los Angeles counties northwestward to Alameda and San Joaquin counties, California.

Seedlings of this species have three (sometimes four) cotyledons, a unique character for North American *Coreopsis*. Largely because of its broad outer phyllaries, relatively large size, leafy stem, and long pappus aristae of the disk achenes, I consider this species to be the most primitive member of section *Pugiopappus*.

4. COREOPSIS BIGELOVII (A. Gray) H. M. Hall, Univ. Calif. Publ. Bot. 3:141. 1907.

TYPE: U.S.A. CALIFORNIA. San Bernardino Co.: On the Mohave Creek, in the desert east [west] of Colorado [River], Mar 1854, *J. M. Bigelow s.n.* (LECTOTYPE, here designated: GH!; ISOLECTOTYPE, here designated: NY!).

Pugiopappus bigelovii A. Gray, Pacif. Railr. Rep. 4:104. 1857.

Pugiopappus breweri A. Gray, Proc. Amer. Acad. 7:660. 1873. TYPE: U.S.A. CALIFORNIA. Ventura Co.: On dry hills at San Buenaventura, *Brewer* 241 (LECTOTYPE, here designated: GH!; ISOLECTOTYPE, here designated: K!).

Leptosyne bigelovii A. Gray, Syn. Fl. N. Amer. 1(2):300. 1884.

Additional specimens examined: U.S.A. CALIFORNIA. Fresno Co.: *Bacigalupi* 6387 (JEPS), 6996 (JEPS); *Constance & Bectle* 2560 (JEPS, UC); *Ferris & Bacigalupi* 13355 (JEPS); *Hoover* 2943 (JEPS, UC); *Jepson* 2763 (JEPS), 15400 (JEPS two sheets); *Kappler* 1851 (LA); *Pauek* 29 (DS); *Wiggins* 12016 (DS, UC). Inyo Co.: *Ferris et al.* 3953 (DS); *Fosberg* S227 (PH), 5295 (PH); 18 Apr 1937, *Kerr s.n.* (CAS); *Pennell & Muntz* 25049 (PH); 15 May 1891, *Schockley s.n.* (UC); *Steward*

& Steward 7380 (ASU); 6 Apr 1937, *Train s.n.* (ARIZ); *Turner* C516 (LA); *Twisselmann* 2553 (CAS). Kern Co.: 18 Apr 1915, *Evermann s.n.* (CAS); *Ferris* 1710 (DS); *Fosberg* S1332 (PH); *Heller* 7662 (PH); *Hood* 39-3* (LA two sheets); *Linsley & MacSwain* 60-21 (UC); *Meng* 516 in part (CAS); *Rose* 48067 (ARIZ), *Smith* 228 (ARIZ), 934 (JEPS); *Twisselmann* 3374 (CAS), 4995 (CAS, JEPS). Los Angeles Co.: *Abrams* 13868 (DS), *Bacigalupi* 4387 (ARIZ, CAS); *Blakley* 2269 (JEPS); *Clokey & Templeton* 4520 (PH, UC two sheets); 27 Mar 1954, *Hogue s.n.* (LA); *Hoover* 3120 (JEPS, UC); 25 Mar 1961, *Lindholm s.n.* (DS); 9 Apr 1936, *McClintock s.n.* (LA); *Smith* 3598 (UARK); *Thompson* 1905 (JEPS); *Tilforth et al.* 1529 (UC); *Twisselmann* 8367 (JEPS). Monterey Co.: *Eastwood* 4022 (CAS). Riverside Co.: *Ray* 1362b (JEPS). San Bernardino Co.: *Alexander & Kellogg* 2009 in part (UC); *Bacigalupi* 6227 (JEPS); *Beal* 11 (JEPS), 742 (JEPS), 777 (JEPS); *Carter* 2305 (DS, LA); *Fosberg* S1687 (PH), S2766 (PH), 5578 (PH), 8213 (PH); 13 Mar 1917, *Hart s.n.* (CAS); *Lewis* 1387 (LA); *Raven* 11936 (JEPS); *Smith* 3575 (UARK); 6 Apr 1937, *Train s.n.* (UARK); *Wolf* 6471 (ARIZ in part, DS, LA), 6533 (ARIZ). San Luis Obispo Co.: *Hoover* 3105 (JEPS), 10455 (ASU), 10493 (UC); *Smith* 3583 (UARK); *Twisselmann* 556 in part (CAS), 1762 (CAS); *Wolf* 6458 (ARIZ, LA). Santa Barbara Co.: *Bittman* 23 (ARIZ); *Elakley* 3454 (JEPS), 4291 (JEPS); 9 Apr 1938, *Epling s.n.* (LA); *Kappler* 2182 (LA); *Smith* 3603 (UARK). Tulare Co.: 27 Mar 1911, *Farr s.n.* (PH); *Ferris* 12174 (DS, UC); *Robbins & Heckard* 3547 (JEPS). Ventura Co.: *DeBuhr & Wainwright* 563 (ASU); 24 Mar 1917, *Evermann s.n.* (CAS); *Kamb & Chisaki* 2212 (ARIZ); *Kappler* 1844 (LA). County not specified: *Coville & Funston* 742 (PH); *Hall* 3027 (DS); 16 May 1903, *Jones s.n.* (DS); *Parish* 226 (PH); 11 May 1882, *Pringle s.n.* (PH); 1882, *Pringle s.n.* (PH); *Smith* 71001 (UARK).

An annual commonly 10–35 cm tall, with leaves mostly or entirely basal, linear outer phyllaries (ca 1.0–1.5 mm wide), medium-sized heads (mostly 2.5–5.5 cm in diameter), chaff attached to the disk achenes, and aristae of the disk achenes ca 1.7–2.8 mm long, of open sandy and shaley soils from Riverside County northwest to Monterey and Fresno counties, California.

Largely because of its narrow outer phyllaries, relatively large size, semiscapose habit, and intermediate-length pappus aristae of the disk achenes, I consider this species to be intermediate evolutionarily in the section.

5. *COREOPSIS HAMILTONII* (Elmer) Sharsmith, *Madroño* 4:214. 1938.

TYPE: U.S.A. CALIFORNIA. Santa Clara Co.: Steep, loose, talus slope on southwest side of tributary canyon to Arroyo Bayo near base of Sugarloaf Mountain, Mount Hamilton Range, altitude 2100 ft, 25 Apr 1936, *H. K. Sharsmith* 3632 (NEOTYPE, here designated: UC!).

Leptosyne hamiltonii Elmer, *Bot. Gaz.* 41:323. 1906. TYPE: U.S.A. CALIFORNIA. Santa Clara Co.: Mount Hamilton, Apr 1900, *A. D. E. Elmer* 2328, not located.

Additional specimens examined: U.S.A. CALIFORNIA. Santa Clara Co.: *Eastwood* 11671 (CAS), 12468 (CAS); *Howell* 4665 (CAS); *Jepson* 4232 (JEPS); *Raven* 10944 (CAS, JEPS); *Sharsmith* 914 (UC), 1709 (UC), 1839 (UC), 3489 (UC), 3942 (UC), 3945 (UC); *Smith* 3580 (UARK). Stanislaus Co.: *Ferris et al.* 13091 (DS); *Rodin* 4928 (DS, UC).

A small (mostly 8–20 cm tall) annual with leaves basal, outer phyllaries

linear (ca 1 mm wide) and reflexed at maturity, small heads (mostly 1.2–1.5 cm in diameter), chaff free from the disk achenes, and aristae of the disk achenes ca 0.9–1.3 mm long, of exposed steep rocky and shaley slopes of Santa Clara and Stanislaus counties, California.

This is a rare species, deservedly listed as rare and endangered in California (Smith, Cole, & Sawyer, 1980) and is in category 2 in the national list of possibly endangered and threatened plants (Federal Register 48 (229):53648. 1983). Largely because of its narrow outer phyllaries, more or less scapose habit, and short pappus aristae of the disk achenes, I consider this species to be the most advanced member of section *Pugiopappus*.

Section EULEPTOSYNE (A. Gray) Blake, Proc. Amer. Acad. 49:341. 1913.

Leptosyne sect. *Euleptosyne* A. Gray, Syn. Fl. N. Amer. 1(2):299. 1844.

TYPE SPECIES: *Coreopsis douglasii* (DC.) H. M. Hall

6. COREOPSIS STILLMANII (A. Gray) Blake, Proc. Amer. Acad. 49:342. 1913.

TYPE: U.S.A. CALIFORNIA. [Probably in Sacramento Co.:] In the valley of the Upper Sacramento [River], *Stillman s.n.* (LECTOTYPE, here designated: GH!; ISOLECTOTYPES, here designated: NY two sheets!, F photograph and fragment!).

Leptosyne stillmanii A. Gray, Bot. Mex. Bound. 92. 1859.

Additional specimens examined: U.S.A. CALIFORNIA. Alameda Co.: 17 Jul 1980, *Rattan s.n.* (DS). Calaveras Co.: without date, *Hermann s.n.* (PH). Contra Costa Co.: Apr 1889, *Brandegee s.n.* (UC). Madera Co.: *Hoover* 821 (JEPS, LA, UC), 4008 (JEPS). Mariposa Co.: *Bacigalupi & Heckard* 9009 (JEPS); *Congdon* 154 (DS); *Crum* 1916 (UC); *Mason* 11125 (UC); *Smith* 3599 (UARK). Placer Co.: *Jepson* 18583 (JEPS); Apr 1865, *Rattan s.n.* (DS). San Joaquin Co.: 11 Mar 1877, *Rattan s.n.* (DS). Santa Clara Co.: *Applegate* 259 (DS); *Breedlove* 4887 (DS, JEPS); *Kamb & Chisaki* 1680 (JEPS); *Sharsmith* 1959 (UC), 3054 (DS, UC); *Smith* 3582 (UARK). Stanislaus Co.: *Carter & Beetle* 1602 (ARIZ, JEPS, PH, UC); *Raven* 18147 (DS); *Sharsmith* 3536 (LA, UC). Tuolumne Co.: *Hoover* 1991 (DS, JEPS, UC); *Jepson* 18072 (JEPS); *Mason* 11019 (DS, LA, UC); *McNeal* 1230 (ASU).

A small (mostly 8–20 cm tall) annual with leaves mostly or entirely basal, the outer phyllaries few glandular-stipitate toothed on the margin basally, small heads (mostly 1.5–3.2 cm in diameter), relatively broad ultimate leaf segments (ca 1–3 mm wide), and achenes with corky wings and dull body, on arid grassy slopes on either side of the Sacramento and San Joaquin vallies from Butte to Tulare and Contra Costa to Stanislaus counties, California (Sharsmith, 1938).

The cotyledons in the achenes of this species are appressed in a plane tangential to the head, the normal orientation, as contrasted to radial plane orientation of the cotyledons in the achenes of the other two species of the section. Largely because of its relatively broad leaf segments, semi-scapose to scapose habit, relatively broader outer phyllaries, and the normal cotyledon

position, I consider this species to be the most primitive one in section *Euleptosyne*.

7. *COREOPSIS DOUGLASII* (DC.) H. M. Hall, Univ. Calif. Publ. Bot. 3:140. 1907 (as to name but not as to description).

TYPE: U.S.A. CALIFORNIA. without locality, *Douglas* 8 (LECTOTYPE, here designated: BM, plant C!; ISOLECTOTYPES, here designated: K two sheets!, GH, plant I!, UC fragment!).

Leptosyne douglasii DC., Prodr. 5:531. 1836.

Coreopsis stillmanii var. *jonesii* Sherff, Bot. Gaz. 97:605. 1936. TYPE: U.S.A. CALIFORNIA. Los Angeles Co.: Pasadena, 2 May 1882, *Marcus E. Jones* 3361 in part (locality in error; see Sharsmith, 1938) (HOLOTYPE: POM!; ISOTYPES: BM!, CAS!, DS two sheets!, NY two sheets!, UC!).

Additional specimens examined: U.S.A. CALIFORNIA. Monterey Co.: 25 Mar 1923, *Bacigalupi s.n.* (DS); *Crum* 1967 (DS, UC); *Eastwood & Howell* 1966 (UC); *Hoover* 2976 (UC), 2988 (JEPS, UC); *Shevock* 1378 (CAS). San Benito Co.: *Burgess* 130 (UC); *Ferris* 8394 (UC); *Keck* 2050 (DS); *Mason* 14733 (UC); *Raven* 10829 (UC). San Luis Obispo Co.: *Eastwood* 13858 (CAS); *Hardham* 4181B (CAS), 5254 (UC), 5518 (CAS); *Hoover* 7482 (DS, UC), 7484 (UC), 7769 (CAS), 9363 (UC); *Smith* 3581 (UARK), 3601 (UARK), 3602 (UARK); *Twisselmann* 2050 (CAS two sheets). Santa Barbara Co.: *Axtlrod* 143 (UC). Santa Clara Co.: *Sharsmith* 3490 (UC), 3627 (DS, UC achenes), 3944 (UC), 15 Jun 1937, *Sharsmith s.n.* (UC).

A small (mostly 6–20 cm tall) annual with leaves entirely basal, the outer phyllaries entire, small heads (mostly 1–3 cm in diameter), narrow ultimate leaf segments (less than 1 mm wide) and achenes with thin wings and shiny, glabrous or nearly glabrous body, on dry rocky and serpentine slopes of the inner South Coast Ranges, from Santa Clara to Santa Barbara counties, California.

The cotyledons of the embryos in the achenes of this species, and the next, are appressed in a plane radial to the head. This unusual orientation links *C. douglasii* and *C. californica* as closely related and is another of the several characters that are similar in the two species. Largely because of its narrow leaf segment width, scapose habit, and its habitat (mountains vs desert), I consider this species to be intermediate (though close to *C. californica*) evolutionarily in section *Euleptosyne*.

- 8a. *COREOPSIS CALIFORNICA* (Nutt.) Sharsmith var. *CALIFORNICA*, Madroño 4:217. 1938.

TYPE: U.S.A. CALIFORNIA: Near San Diego, Upper California, Nuttall s.n. (LECTOTYPE, here designated: BM, upper three plants!; ISOLECTOTYPE, here designated: PH, two plants at upper left!).

Leptosyne californica Nutt., Trans. Amer. Phil. n. ser. 7:363. 1841.

Additional specimens examined: U.S.A. CALIFORNIA. Inyo Co.: *Twisselmann* 7102 (CAS two sheets, JEPS). Kern Co.: *Cantelow* 2130 (CAS); May 1927, *Epling s.n.* (LA); *Fosberg* S1333 (PH); 7 Apr 1932, *Hilend s.n.* (LA); *Hitchcock* 5825 (CAS);

29 May 1936, *Humphrey s.n.* (ARIZ); *Jepson* 15440 (JEPS), 15570 (JEPS); *Thomas* 7623 (JEPS); *Twisselmann* 10655 (JEPS). Los Angeles Co.: *Bacigalupi* 4818 (JEPS); *Baker* 5325 (UC), 20 May 1909, *Baker s.n.* (DS); *Ernst* 231 (UC); *Ferris & Rossbach* 9482 (LA); *Grant* 681 (PH), 682 (ARIZ); *Henrickson* 5527 (ASU); *Johnson* 3979 (LA two sheets); *Jones* 3373 (CAS); *Keil* 11891 (ASU); *Smith* 3597 (UARK); *Strother* 614 (UC); *Wiggins* 20590 (DS); *Wiggins & Ernst* 231 (UC); *Wolf* 8520 (ARIZ, DS, LA). Orange Co.: May 1899, *Bowman s.n.* (DS). Riverside Co.: *Apton* 171 (ASU); *Cooper* 1024 (ARIZ, LA); *Fosberg* S1706 (PH); *Hitchcock & Mublick* 23091 (DS); *Howell* 1232 (UC); *Raven* 11870 (JEPS); *Rose* 49061 (ARIZ, UC); *Spencer* 653 (PH); *Terrell* 71 (ASU); *Tilforth et al.* 1502 (UC). San Bernardino Co.: *Alexander & Kellogg* 2009 (in part UC); *Eastwood* 18661 (CAS); 11 May 1936, *Epling & Stewart s.n.* (LA); *Everett & Balls* 23073 (CAS); *Ferris & Bacigalupi* 13194 (DS); *Fosberg* S1684 (PH), S2815 (PH); *Gould* 904 (PH); 24 Apr 1937, *Grant s.n.* (LA); *Heller* 7674 (PH); *Holmgren & Holmgren* 7610 (ASU); *Jepson* 12634 (JEPS); *Kappler* 1102 (LA), 1613 (LA), 2048 (LA); *Keil* K12397 (ASU); 24 Feb 1935, *Krames s.n.* (JEPS); Apr 1878, *Lemmon s.n.* (JEPS); 24 Apr 1938, *Lewis s.n.* (LA); *Raven* 11896 (JEPS); *Shreve* 8172 (ARIZ two sheets); *Smith* 3576 (UARK); *Tilforth & Dourley* 362 (ASU); *Wiggins* 13375 (ARIZ, DS, UC); *Wolf* 6471 in part (ARIZ), 6505 (ARIZ, LA). San Diego Co.: *Abrams* 3628 (DS, PH); *Brandege* 3368 (DS); *Clements & Clements* 224 (PH two sheets), 225 (PH two sheets); *Glownke* 4661 (PH); *Jepson* 8529 (JEPS), 8677 (JEPS), 11819 (JEPS); 7 Feb 1884, *Orcutt s.n.* (PH); 4 Apr 1937?, *Rowntree s.n.* (CAS); *Smith* 3588 (UARK); *Spencer* 172 (PH). Tulare Co.: 29 Mar 1911, *Farr s.n.* (PH); 30 Mar 1937, *Winblad s.n.* (CAS). Ventura Co.: *Kappler* 283 (LA). County not specified: Apr 1905, *Brandege s.n.* (PH); *Parish & Parish* 620 (PH); May 1903, *Saunders s.n.* (PH), Apr-May 1906, *Saunders s.n.* (PH); May 1904, *Williamson s.n.* (PH two sheets). MEXICO. Baja California: *Carter et al.* 1049 (ARIZ); 15 Feb 1935, *Epling & Robison s.n.* (ARIZ, LA, UC); *Hall* 3973 (UC); *Lewis & Thompson* 12163 (UC); *Moran* 16871 (ARIZ), 20807 (UC); *Palmer* 677 (ARIZ, UC); *Raven et al.* 12561 (CAS, LA, UC); *Wiggins* 9792 (DS).

An annual commonly 10–30 cm tall, with leaves entirely basal, the outer phyllaries entire, small heads (mostly 1.5–3.5 cm in diameter), narrow ultimate leaf segments (about 1 mm or less in width) and achenes with corky wings and dull body with many tiny clavellate trichomes, on sandy and gravelly desert plains and washes of southern California from San Diego County north and west to Inyo, Tulare, and Ventura counties and of Baja California, Mexico.

This species was confused with *C. douglasii* for many years, and was first clearly distinguished from that species by Sharsmith (1938). *Coreopsis californica* was the subject of a recent paper (Smith, 1983) in which a new variety was named. While normally having epappose achenes, individuals of the species rarely exhibit achenes with two thin, antrorsely hispidulous aristae. Largely because of its narrow leaf segments, scapose habit, and its habitat (desert vs mountains), I consider *C. californica* to be the most advanced species of section *Euleptosyne*.

8b. *COREOPSIS CALIFORNICA* var. *NEWBERRYI* (A. Gray) E. B. Smith, *Brittonia* 35:168. 1983.

TYPE: U.S.A. ARIZONA: Sitgreaves [Sitgravis] Pass, Colorado [River], 26 Mar, *Dr. Newberry s.n.* (LECTOTYPE, here designated: GH!). This type was improperly called the holotype in my earlier paper (Smith, 1983).

Leptosyne newberryi A. Gray, Proc. Amer. Acad. Arts 7:358. 1868.

Additional specimens examined: U.S.A. ARIZONA. Gila Co.: 9 Mar 1940, *Nichol s.n.* (ARIZ); *Palmer 126* (GH), Apr 1932, *Palmer s.n.* (CAS). Graham Co.: *McGill LAM2341* (ASU); *Mcguire et al 19173* (ARIZ); *Smith 3596* (UARK). Maricopa Co.: 14 Mar 1937, *Darrow s.n.* (ARIZ). Mohave Co.: 15 Mar 1931, *Braem s.n.* (DS); *Peebles 11281* (ARIZ). Pinal Co.: *Gillespie 5420* (AS, DS, UC); *Haase et al. 712* (ARIZ); *Lehto 17970* (ASU); *Peebles et al. 858* (ARIZ), *5172* (ARIZ, LA two sheets); *Smith 3595* (UARK); *Sundell et al. 11725* (ASU).

A variety differing from the typical one in achene characters (see key), of gravelly floors of desert washes in southeastern Arizona (Gila, Maricopa, Pinal and Graham counties; also known from one local area in southern Mohave County).

This variety replaces the typical variety in Arizona (Smith, 1983). The varieties of *C. californica* show maternal inheritance of the achene spot pattern. Despite the larger achenes of var. *newberryi*, its peripheral range compared with other taxa in the section suggests that it is more recently derived than var. *californica*; it is probably the most advanced taxon in section *Euleptosyne*.

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